

# 11 Bat flies - obligate ectoparasites of bats

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## 1 Introductory remarks

Bat flies (Diptera: Hippoboscoidea) are highly specialized ectoparasites and only associate with bats (Mammalia: Chiroptera). They live in the fur and on the wing membranes where they feed on host blood. Bat flies are nominally divided into two cosmopolitan families, Streblidae and Nycteribiidae, but recent phylogenetic studies suggest these are not natural groups (Dittmar et al. 2006). Nycteribiids (275 species) are more speciose in the Eastern Hemisphere, whereas the streblids (227 species) are richer in the Western. Generally, both families are most diverse in the tropics, less diverse in subtropics, and rather impoverished in temperate regions. However, this latitudinal richness gradient is more pronounced in the Western Hemisphere. *Mystacinobia zelandica* (Mystacinobiidae) has been considered a “bat fly” (Holloway 1976). This fly is a roost associate with and phoretic on the endemic New Zealand bat *Mystacina tuberculata*. Unlike members of the Nycteribiidae and Streblidae, *M. zelandica* feeds on guano, not host blood. Molecular analysis places *M. tuberculata* within the Oestroidea (Gleeson et al. 2000). This chapter summarizes current understanding of the taxonomy, life history, and breeding biology of flies allocated to Streblidae and Nycteribiidae, and offers overviews of morphology, behavior, specificity, ecology, and cospeciation in the context of the parasite-host association.

## 2 Taxonomy

Together with the families Hippoboscidae (bird flies, ked flies) and Glossinidae (tsetse flies), bat flies belong to the dipteran superfamily Hippoboscoidea. This group of “pupiparous” flies represents one of the most derived clades of Diptera (Yeates and Wiegmann 1999), with highly modi-

fied development and peculiar life histories. Although phylogenetic analyses of the group are still preliminary, the two bat fly families appear to be monophyletic, sister to either bird flies or tsetse flies. Recognized families of bat flies are small relative to other dipteran families: Streblidae are worldwide in distribution and include 5 subfamilies, 32 genera, and 227 described species. Whereas streblids are found in both Eastern and Western Hemispheres, they largely inhabit tropical and subtropical regions and are more speciose in the West (156 species) than in the East (71 species; Whitaker et al., in press). No species, genus or even subfamily is distributed in both hemispheres. Eastern forms include the Nycteriboscinae (4 genera, 50 species) and the Ascodipterinae (2 genera, 21 species). Western forms include the Nycterophiliinae (2 genera, 6 species), Streblinae (4 genera, 35 species), and Trichobiinae (19 genera, 115 species). All five species of the streblid genus *Megastrebla* (Nycteriboscinae) are associated with pteropodid bats (exclusively Eastern), but the remaining species in the family are associated with the Microchiroptera. In the American tropics, streblids are by far the most diverse upon the bat family Phyllostomidae.

The Nycteribiidae includes 3 subfamilies, 12 genera, and 275 described species. Although species are found in tropical and subtropical regions worldwide, they are richer in the Eastern Hemisphere (222 species versus 53 species in the Western). No nycteribiid species is found in both Eastern and Western Hemispheres. Two subfamilies, Archinycteribiinae (1 genus, 3 species), and Cyclopodiinae (4 genera, 62 species) are exclusively Eastern Hemispheric in distribution, where they associate with Pteropodidae. The Nycteribiinae (7 genera, 210 species) are cosmopolitan in distribution and mainly associated with the families Vespertilionidae and Rhinolophidae. The most species-rich genus, *Basilina*, is also cosmopolitan and comprises 122 nominal species. *Basilina* species are mainly found in association with the Vespertilionidae, but also with the Phyllostomidae. All four species of *Hershkovitzia*, the only genus restricted to the Americas, parasitize bats of the endemic family Thyropteridae.

### 3 Life history and breeding biology

Little is known regarding life history and reproductive biology of bat flies. Generalizations are based on limited studies of a few species. Generally, all bat flies reproduce via viviparous puparity (Hagan 1951), in which eggs are fertilized internally and all larval stages develop within the female, nourished by intrauterine "milk" glands. Larvae moult twice inside the female, and gravid females deposit a single, terminal (3rd-instar) larva on the

roosting substrate. Once deposited, the larva (referred to as a prepupa) immediately forms a puparium. Following a pupal stage that lasts 3-4 weeks (Ching and Marshall 1968), an adult fly emerges and must locate and colonize a host. Prepupal deposition directly on the host's body has been reported, but the pupae were distorted in shape and most failed to develop into an adult fly. Left on the bats, most pupae were groomed off by the host (Ching and Marshall 1968). In general, the life-history strategy of bat flies reflects their obligate association with bats: vulnerable immature stages remain coupled with the host inside the female fly.

Peterson and Wenzel (1987) suggested that the life cycle of nycteribiids is rather uniform. The life cycle of *Basilina hispida* has been described in some detail (Marshall 1970). Flies reached sexual maturity 5-6 days after emergence from the puparium. Males usually copulated with females immediately following prepupal deposition, but sometimes with newly emerged females. A single copulation was sufficient to produce several offspring, suggesting that females store sperm. At 9-day intervals, mature females deposited prepupae on roost substrate, pressed into place with their abdomens. Prepupal deposition occurred between 0900 and 1800 hours, while bats were in their roosts, stimulated largely by elevated temperature. From 25 to 46 days later, with host bats present or absent from the roost, respectively, wingless, teneral adults emerged and randomly walked about until encountering a host. Upon colonizing a host, flies began feeding within 20 min. *Basilina hispida* died within 5-25 hours of being removed from a host, with new mother flies dying sooner and teneral flies dying later. The total life-span of *B. hispida* averaged 136 and 195 days for males and females, respectively, with 5 days pre-partum, 9 days in the larval stages, 25 days in puparium, and 97 days (males) or 156 days (females) in the adult stage (Marshall 1970).

The breeding biology of *Eucampsipoda sundaica* was described by Ching and Marshall (1968). Most features of the life cycle resembled that of *B. hispida*, but during mating, males attached to females for up to 1/2 hour, during which time the female remained fully ambulatory. The interval between successive prepupal depositions was three times faster in *E. sundiaca* than *B. hispida* (3 versus 9 days, respectively). It was noted that some *E. sundiaca* prepupae were deposited directly on the host, but these pupae were distorted in shape and easily removed by the bat (Ching and Marshall 1968).

Life histories of streblid species likewise are poorly known and described for only a few species. The most detailed is Overal's (1980) study of the life cycle of *Megistopoda aranea* from Panama. In this species, prepupae were deposited in the roost, usually near bats. Following about 23 days, the adult emerged from the puparium and located a host for a blood

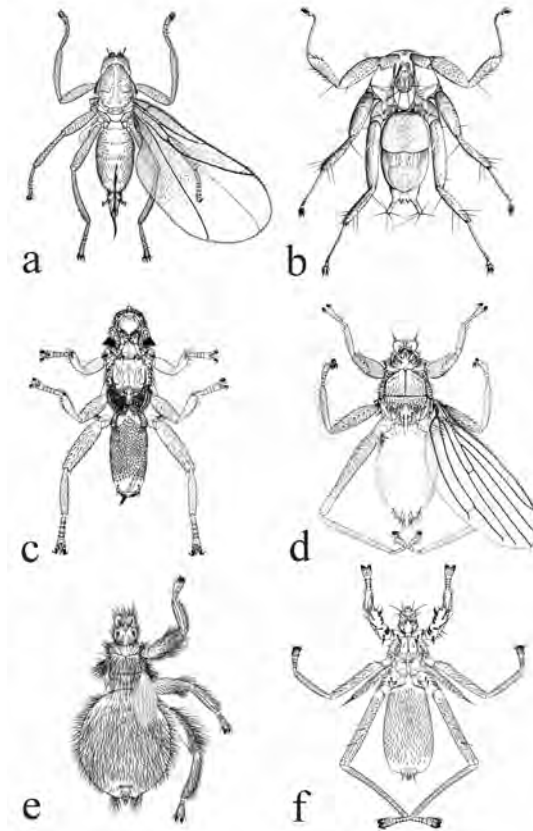
meal before mating. However, females were observed mating only minutes after depositing the prepupa. The time interval between successive depositions of prepupae was about 10 days. Fritz (1983) studied *Trichobius joblingi*, *Speiseria ambigua*, and *Strebla guajiro* in Costa Rica. These species also deposited their prepupae on roost substrates and away from the host, and the pupal stage lasted about 17, 20, and 19 days for these fly species, respectively. A few studies have been conducted on temperate (North American) streblid species. Generally, life histories of temperate species resemble those in tropical regions. However, bat flies remain physically and reproductively active on hibernating bats whose body temperatures ranged from 2-6 degrees C (Ross 1960; Reisen et al. 1976; Caire and Hornuff 1986).

Females of the streblid *Ascodipteron* embed in the skin of their hosts and become endoparasitic (Maa 1965), whereas males (Fig. 1a) are external parasites. Female *Ascodipteron* are the only exception to the ectoparasitic nature of bat flies. Basic life-history details are available for only two species. In *A. namrui*, duration of the pupal stage ranged from 24-35 days, whereas the interval between successive depositions of prepupae ranged from 2-8 days at 26-30° C (Maa 1965). In another species, *A. rhinopomatos*, the pupal duration was nearly equal to *A. namrui* (Theodor and Moscona 1954), but the interval between prepupal depositions was longer, ranging from 6-13 days (Maa 1965).

#### 4 Morphology and behavior

Nycteribiids are completely wingless and spider-like in appearance (Fig. 1b). Although species vary greatly in size (1.5-5.0 mm), their overall aspect is rather similar across the species. Their flight muscles are atrophied, which in turn reduces the overall bulk of the thorax. Their legs and small head all protrude from the dorsal thoracic surface, and the insects are somewhat dorsoventrally flattened. All species possess a head that is folded back against the thorax when at rest. When feeding, the head rotates nearly 180 forward and downward (Peterson and Wenzel 1987). *Basilina hispida* and three species of Central American *Basilina* have been observed only on furred regions of their hosts (Marshall 1971; ter Hofstede et al. 2004). Our observations of other nycteribiids, including *Hershkovitzia* spp., support that observation. Like fleas, nycteribiids possess several ctenidea or combs. The ctenidia are thought to facilitate host attachment, preventing the animal from being brushed backwards from the fur (Traub 1972; Amin 1974), not for protection from abrasive action of host hair

(Marshall 1980a, 1981). Nycteribiids generally move equally well in any direction, and their movements may be very fast when agitated. Such frenetic mobility may allow them to evade host grooming, inferred to be the greatest cause of mortality in adult bat flies (Marshall 1981). When feeding, nycteribiids thrust their bodies downward into the fur. Their mouthparts contact the host's skin and the tip of their abdomen is generally visible at this time.



**Fig. 1.** Representative genera of bat flies. (a) *Ascodipteron africanum* (Streblidae: Ascodipterinae), male, dorsal view, modified from Jobling (1940); (b) *Styldia biarticulata* (Nycteribiidae: Nycteribiinae), female, dorsal view, modified from Theodor (1967); (c) *Metelasmus pseudopterus* (Streblidae: Streblinae), male, dorsal view, modified from Jobling (1936); (d) *Speiseria ambigua* (Streblidae: Trichobiinae), female, dorsal view, modified from Jobling (1939); (e) *Anatrichiobius scorzai* (Streblidae: Trichobiinae), female, dorsal view, from Wenzel et al. (1966); (f) *Neotrichobius stenopterus* (Streblidae: Trichobiinae), female, dorsal view, from Wenzel et al. (1966) (reprinted with permissions from the Field Museum of Natural History, Cambridge University Press and Prof. Yosef Shlein)

The Streblidae also vary greatly in size, with total length generally 1.5-2.5mm, but ranging from 0.73mm (e.g., *Mastoptera minuta*, the smallest bat fly) to 5.50mm (e.g., *Joblingia schmidti*). In contrast to the conservative body plan of nycteribiids (Fig. 1b), streblids possess radically different body plans from strongly laterally compressed (e.g., Nycterophiliinae) to dorsoventrally flattened (e.g., Streblinae; Fig. 1c) to uncompressed (e.g., most Trichobiinae; Figs. 1d-1f) (Wenzel et al. 1966; Dick and Miller, in press). The nycterophiliine species are laterally compressed and resemble fleas in overall morphology and in their movements through hair. The strong and rapid “swimming” movement of these insects makes them especially difficult to capture alive on the host (Dick, personal observations). Other differences among streblid species include extremely elongated legs in some genera of trichobiines (Figs. 1d, f) and a well-developed ctenidium (Fig. 1c) in all species of streblines. Observations of living flies reveal that the long-legged species run across the top of the host’s fur. These species are accordingly the most conspicuous parasites when bats are handled. Behaviors of species (e.g. *Strebla* spp.) that possess a ctenidium along the posteroventral margin of the head (Fig. 1c) have been observed in glass vials: when these flies elevate the head, a large gap is formed between the ctenidium and the anteroventral margin of the thorax, which can be clamped closed when the fly pronates the head downward (Dick, personal observations). When on a host, such a motion would secure the fly to the host by grasping host hair within this ctenidior thoracic gap. In all the bat flies we have handled, the most important structures for host attachment appear to be tarsal claws. When streblids are collected alive from the host, nearly always their final and strongest resistance to capture involves grasping hairs or wing membrane with flexed tarsal claws. Attempts to aspirate live flies from hosts failed; flies tightly grasped the host hairs with their tarsal claws (Dick, personal observations).

Although all nycteribiids are wingless (Fig. 1b), most (220 species or 97%) streblids possess wings, but not all these possess functional, macrop-terous wings (Figs. 1a, d). Of the winged species, 24 species (10.9%) possess non-functional vestigial wings, 7 species the stenopterous form (Fig. 1f) and 17 the brachypterous form (Figs. 1c, e) (Dick and Miller, in press). The remaining 6 species (*Paradyschiria* and *Phalconomus puliciformis*) are apterous, with *Paradyschiria* spp. lacking halters as well. Typically even the fully winged forms are rather weak flyers, but species vary in their proclivity to fly when disturbed. Species of Ascopidterinae are unique among bat flies in that, upon attachment to a host bat, alate females immediately shed their wings, halters, and all leg segments beyond the coxae (Hastriter et al. 2006). The thorax and mouthparts invaginate within the abdomen, and most of the insect is enveloped by host dermal tissue. Only

the membranous terminal segments remain exposed. In these flies, attachment occurs on the host's wings, behind the ears, or in the urogenital areas. Thus, females of these species are effectively endoparasites (Hastriter et al., in press).

Adult bat flies typically reside with the host. Females leave the host only to deposit their prepupa, usually on the walls of the roost. Only *Ascodipteron* species are known to deposit their prepupa on the ground, similar to Hippoboscidae and Glossinidae (Maa and Peterson 1987; Jordan 1993). Males were thought not to leave the host at any time. However, in a Puerto Rican cave roost of *Artibeus jamaicensis*, Dick observed both pupae and adults of *Trichobius intermedius* (Streblidae) on the walls of the cave, even after the bats had departed for the night. Adult flies were observed walking among both pupae and pupal exuviae. Of 23 adult flies collected from the roost wall in vicinity of the pupae, 11 were males and 12 females (Dick, unpublished data), so that both males and females leave the host for at least brief periods.

## 5 Host associations and ecology

As with most obligate parasites, the lives of bat flies are tightly coupled with those of their hosts. Consequently, geographical distributions of bat fly species closely mirror those of their host species (Wenzel et al. 1966; Wenzel 1976). No verified records of bat fly species are known from locations outside the range of their primary host species.

### 5.1 Autecology

Autecological studies have been undertaken on very few bat fly species. The autecology of *Basilina hispida* (Nycteribiidae) was studied by Marshall (1971). In Malaysia, *B. hispida* is known to associate with two species of vespertilionid bats, *Tylonycteris pachypus* and *T. robustula*. However, prevalence of infestation differed between the two host species; prevalence for 707 *T. pachypus* was 34.8% but only 9.6% for 597 *T. robustula*. In captivity, *B. hispida* lived and reproduced successfully on either sex of either bat species. Flies readily dispersed among bat individuals, but given time, ultimately congregated on *T. pachypus*. Consequently, *T. pachypus* was considered the preferred host and *T. robustula* a secondary host (Marshall 1971). Males of both host species more often harbored parasites than did females. This defies conventional wisdom – females often have higher prevalence and intensity of parasite infestation, purportedly because they

offer more dependable vertical transfer of ectoparasites from adult hosts to their offspring.

## **5.2 Effect of roosting dynamics**

Bat species achieve remarkable diversity in the tropics, with local richness in excess of 86 species (e.g., Lim and Engstrom 2004). Such diversified assemblages roost in comparably diversified locations (Kunz and Lumsden 2003), either singly, in social groupings, or in multi-specific associations, some of which are fairly characteristic. Such roosting dynamics of bats appear to be crucial to the ecology of parasitic bat flies. Jobling (1949) believed that bat flies lacked host specificity because multiple bat species often utilize a common roost – the flies effectively use all individuals in the spatially confined roost as one large host population. In fact, he supposed that the polyxenous nature of several bat fly species had evolved due to selective pressures surrounding multiple-species roosts (Jobling 1949). Host population size has been supposed to affect the prevalence and intensity of bat fly infestation, but to date such assertions have only been anecdotal. High densities of host bats would provide a rich substrate for bat flies to feed, and would provide many options for colonization by newly emerged adult flies. Conversely, bats that roost solitarily or in small groups provide limited substrate for bat flies. Over evolutionary time, such pressures should select for dense populations of bat flies on high-density roosters of large colonies, and would discourage robust populations of bat flies on solitary roosting species, or those that roost in small colonies. Bat flies occurring on Belizean bat species were evaluated by ter Hofstede and Fenton (2005). Bats that used cavities as the primary roost structure were hypothesized to support higher densities of bat flies than bats roosting in foliage. Although independent contrasts were impossible because a bat fly phylogeny is lacking, host species known to be cavity roosters had significantly higher parasite loads than those classified as foliage roosters (ter Hofstede and Fenton 2005).

## **5.3 Multiple species infestation**

Bats species often are infested with several bat fly species (Wenzel et al. 1966; Wenzel 1976; Dick and Gettinger 2005). Multiple species parasitization has been documented for both nycteribiids (Whitaker et al., in press) and streblids (Wenzel et al. 1966). However, such patterns have been investigated only among American streblids. Bat species in Venezuela are infested with 0-4 bat fly species; 63% of infested bats hosted 2-4 fly spe-

cies (Wenzel 1976). Presence-absence analysis revealed that observed combinations of bat fly species occur together more often than expected by chance (Dick 2005). Co-occurring fly species were typically associated positively rather than negatively, so that a high abundance of one species was significantly correlated with a high abundance of the other species (Dick 2005). These results may indicate a mutualistic relationship among co-occurring flies, and contrast with some other parasite co-occurrence studies, in which density compensation seems to be the rule (Gotelli and McCabe 2002; Gotelli and Rohde 2002; Fellis et al. 2003).

Host grooming appears to be the principal cause of insect ectoparasite mortality (Marshall 1981). Grooming pressure may constitute an important selective factor driving the evolution of host-limited parasites. Parasites may become specialized to particular spatial locations or ecological niches due to host grooming behavior (Reiczigel and Rozsa 1998). Plausibly, both the presence and abundance of other parasite species would lessen host grooming pressure on a given species of bat fly. The presence and higher abundance of one parasite species would facilitate the presence and abundance of the other, by reciprocally redirecting grooming pressure from each other. This scenario is similar to that of Reiczigel and Rozsa (1998) who modeled the persistence of two species of parasites on a host over time. Meaningfully, positively associated fly species invariably belonged to different genera (Dick 2005). Different morphologies of co-occurring species may facilitate resource subdivision, including spatial segregation of parasites (ter Hofstede et al. 2004).

#### **5.4 Host specificity**

Host specificity gauges the degree to which a parasite species is restricted to a particular host species (Poulin 1998). The degree to which bat flies are host specific has long has been debated (Jobling 1949; Theodor 1957, Wenzel et al. 1966; Marshall 1981; ter Hofstede et al. 2004; Dick and Gettinger 2005). Early studies concluded that bat flies were not highly host specific, presumably because many bat species typically roost together and share a common pool of parasites (Jobling 1949; Theodor 1957). In Panama, 55% of bat fly species were associated with a single host species, while another 15% appeared to be monoxenous but were sometimes recorded on other hosts (Wenzel et al. 1966). In Malaysia, Marshall (1980b) reported that 72% of streblids and 64% of nycteribiids were recorded from a single host, with additional flies restricted to sets of congeneric species. In a study specially designed to eliminate cross-host contamination of parasites, Dick and Gettinger (2005) showed that 99.4% of the 2,467 flies

taken in their Paraguayan survey were associated with primary bat host species. All but one of the 15 mismatches resulted from sampling contamination (Dick, unpublished data). Generally, results of modern controlled surveys suggest very high host specificity among bat flies (ter Hofstede et al. 2004; Dick and Gettinger 2005).

The ability to fly presumably is an important factor in the degree of host specificity, with flightless species being more host specific, and winged species being less specific (Jobling 1949). In general, flightless species only able to crawl from host to host should be more host-limited than flying species that may easily move from host to host over great distances. However, nycteribiids appear to be no more host-specific than streblids (Marshall 1980b), despite all being flightless while few streblids are. Recently, ter Hofstede et al. (2004) suggested that mobility has no effect on the degree of host specificity among Belizean bat flies.

Marshall (1976) regarded both families of bat flies as being host specific, with species parasitizing usually one host species, or sometimes two or more species of a given host genus. The degree of host specificity was attributed to many factors, including physical isolation, climate, competition, predation, and morphological and physiological adaptation (Marshall, 1976). Not mentioned were evolutionary responses to host-parasite cospeciation (Clayton et al. 2003; Hugot this volume). Combes (1991) outlined the Filter Concept (FC) in an attempt to explain the evolution of parasite life cycles. The FC encompasses Marshall's (1976) factors listed above. The FC has direct application to the evolution of host specificity. The Encounter Filter excludes potential hosts that the parasite cannot encounter and colonize for behavioral or ecological reasons. The Compatibility Filter excludes host individuals on which the parasite cannot survive due to morphological, physiological, or immunological reasons. The filters together represent selective pressures for the parasite, acting to increase or decrease host specificity (Combes 1991). However, the FC does not account for the parasite's ability to encounter mates and reproduce successfully. Due to cospeciation, lineages of bat flies become reproductively isolated on respective host lineages. Such isolation should also maintain selection for continued specificity on the basis of mate availability; in brief, bat flies are specific to their hosts because that is where they are able to reproduce. This represents a Reproductive Filter for the evolution of host specificity (Dick, unpublished data).

## 6 Effect of parasites on hosts

While bat roosting dynamics affect the ecology of fly parasites, bat fly parasitism also affects the host mammals. Parasitism is a symbiotic relationship in which one of the participants (the parasite) harms the other participant (the host) or otherwise lives at the expense of the other participant (Roberts and Janovy 2000). Some parasites are quite harmful to their host, whereas the harmful effects of others can scarcely be measured. Although bat fly bites are painful to humans, host bats exhibit no reaction to the nearly constant feeding of bat flies (Wenzel et al. 1966; Dick, personal observations). Bat fly bites do not cause sores or lesions on the bat's skin as they do on humans. Grooming effort by captive bats of one species does not differ depending on the intensity of bat fly infestation. However, bat species with higher parasitism levels groomed more intensely than those host species with lower parasitism rates (ter Hofstede and Fenton 2005). Grooming is a costly behavior for bats (Kunz 1982) and increased grooming may affect the host's time budget for other crucial activities such as foraging for food. Regarding a tangible effect on hosts, parasitism by *Megistopoda proxima* (Streblidae) was correlated with significant weight loss in male *Sturnira lilium* (Linhares and Komeno 2000).

Parasitism may also affect the site fidelity of bats, as has been shown for other host species such as barn swallows (Barclay 1988). Bat flies deposit their prepupae inside the roost, and newly emerged flies depend on the presence of host bats. Moving to a different roost before the adult flies emerge may be an effective means for bats to lower both prevalence and intensity of ectoparasite infestation (Lewis 1995).

## 7 Phylogeny and cospeciation patterns

Comprehensive, robust phylogenies are lacking for Nycteribiidae and Streblidae, and their relationships to other hippoboscoid flies are poorly understood. There is strong support for monophyly of the Hippoboscoidea (McAlpine 1989; Yeates and Wiegmann 1999; Nirmala et al. 2001; Dittmar et al. 2006). Earlier notions that Streblidae and Nycteribiidae each were monophyletic (McAlpine 1989) were challenged by a molecular analysis of the calypterate Diptera (Nirmala et al. 2001). An expanded analysis based on additional genes argued that bat flies are monophyletic, but that the two principal subdivisions do not follow classical lines. Instead, the Western Hemisphere Streblidae constitute one clade and Eastern Hemisphere Streblidae plus Nycteribiidae comprise another (Dittmar et al.

2006). That conclusion is being reanalyzed using several additional genes and a taxon-dense sampling approach (Dittmar, personal communication). Patterson et al. (1998) provided distributional evidence that bat flies have cospeciated with their bat hosts, finding related groups of flies on host clades. Bat fly families, genera, and species groups often are restricted to particular host families, subfamilies, and genera (Wenzel and Tipton 1966; Wenzel et al. 1966). Additional phylogenetic studies of bat flies are urgently needed to extend current knowledge on many topics.

## **8 Bat flies as vectors of zoonoses**

As blood-feeding parasites, bat flies would appear excellent vectors of zoonoses. Generally high degrees of host specificity (Marshall 1976; Dick and Gettinger 2005) diminish the likelihood of interspecific transfer of bat diseases and pathogens. However, it is likely that bat flies transmit species-specific pathogens within host populations. Both nycteribiid and streblid species are known to infest *Hypsignathus monstrosus*, *Epomops franqueti*, and *Myonycteris torquata*, three species of Old World fruit bats (Megachiroptera: Pteropodidae). Recent evidence suggests that species of pteropodids may harbor the deadly Ebola virus (Leroy et al. 2005). It is possible that parasitic bat flies not only transfer such viruses among host bats, but given that bat flies occasionally bite humans (Wenzel et al. 1966; Dick, personal observations), it is theoretically possible that bat flies could transmit Ebola to humans.

## **8 Concluding remarks**

Bat flies are highly specialized for a nearly permanent ectoparasitic relationship with their hosts, the Chiroptera. Although known life-histories are rather similar across all taxa, bat flies exhibit a variety of morphological adaptations, most suiting them for the two physical substrates offered to them by their bat hosts, the fur and the flight membranes. These morphological adaptations and the ecological diversity of their hosts make bat flies an excellent group in which to study the parasitic relationship, including morphological accommodations, cospeciation, and coevolution.

## References

- Amin OM (1974) Comb variations in the rabbit flea *Cediopsylla simplex* (Baker). *J Med Entomol* 11:227–230
- Barclay RMR (1988) Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). *Auk* 105:53–60
- Caire W, Hornuff L (1986) Overwintering population dynamics of the bat fly *Trichobius major* (Diptera: Streblidae). *Southwest Nat* 31:126–129
- Ching LM, Marshall AG (1968) The breeding biology of the bat-fly *Eucampispora sundaicum* Theodor, 1955 (Diptera: Nycteribiidae). *Malayan Nat J* 21:171–180
- Clayton DH, Al-Tamimi S, Johnson KP (2003) The ecological basis of coevolutionary history. In: Page RDM (ed) *Tangled trees: Phylogeny, cospeciation, and coevolution*. Univ Chicago Press, Chicago, pp 310–341
- Combes C (1991) Evolution of parasite life cycles. In: Toft CA, Aeschlimann A, Bolis L (eds) *Parasite-host associations: Coexistence or conflict?* Oxford Univ Press, Oxford, pp 62–82
- Dick CW (2005) Ecology and host specificity of bat flies (Diptera: Streblidae) and their chiropteran hosts. Ph. D. Thesis, Texas Tech University
- Dick CW, Gettinger D (2005) A faunal survey of streblid bat flies (Diptera: Streblidae) associated with bats in Paraguay. *J Parasitol* 91:1015–1024
- Dick CW, Miller J (in press) Streblidae. In: Brown BV (ed) *Diptera of Central America*. Los Angeles Co Mus Nat Hist, Los Angeles
- Dittmar K, Porter ML, Murray S, Whiting MF (2006) Molecular phylogenetic analysis of nycteribiid and streblid bat flies (Diptera: Brachycera, Calyptratae): Implications for host associations and phylogeographic origins. *Mol Phyl Evol* 38:155–170
- Fellis KJ, Negovetich NJ, Esch GW, Horak IG, Boomker J (2003) Patterns of association, nestedness, and species co-occurrence of helminth parasites in the greater Kudu, *Tragelaphus strepsiceros*, in the Kruger National Park, South Africa, and the Etosha National Park, Namibia. *J Parasitol* 89:899–907
- Fritz GN (1983) Biology and ecology of the bat flies (Diptera: Streblidae) on bats of the genus *Carollia*. *J Med Entomol* 20:1–10
- Gleeson DM, Howitt RLJ, Newcomb RD (2000) The phylogenetic position of the New Zealand batfly, *Mystacinobia zelandica* (Mystacinobiidae: Oestroidea) inferred from Mitochondrial 16S ribosomal DNA sequence data. *J R Soc New Zeal* 30:155–168
- Gotelli NJ, McCabe DJ (2002) Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83:2091–2096
- Gotelli NJ, Rhode K (2002) Co-occurrence of ectoparasites of marine fishes: A null model analysis. *Ecol Lett* 5:86–94
- Hagan HR (1951) *Embryology of the viviparous insects*. Ronald Press, New York
- Hastriter MW, Dittmar K, Whiting MF (2006) Investigation of taxonomically important morphological features of endoparasitic bat flies of the subfamily As-

- codipterinae (Streblidae) by scanning electron microscopy. *Zootaxa* 1122:57-68
- Holloway BA (1976) A new bat-fly family from New Zealand (Diptera: Mystaciboliidae). *New Zeal J Zool* 3:279-301
- Jobling B (1936) A revision of the subfamilies of the Streblidae and the genera of the subfamily Streblinae (Diptera Acalypterae) including a redescription of *Metelasmus pseudopterus* Coquillett and a description of two new species from Africa. *Parasitology* 28:355-380
- Jobling B (1939) On some American genera of the Streblidae and their species, with the description of a new species of *Trichobius* (Diptera: Acalypterae). *Parasitology* 31:486-497
- Jobling B (1940) Description of the young female and of the male of *Ascodipteron africanum* Jobling (Diptera: Streblidae). *Parasitology* 32:399-400
- Jobling B (1949) Host-parasite relationship between the American Streblidae and the bats, with a new key to the American genera and a record of the Streblidae from Trinidad, British West Indies (Diptera). *Parasitology* 39:315-329
- Jordan AM (1993) Tsetse-flies (Glossinidae) In: Lane RP, Crosskey RW (eds) *Medical insects and arachnids*. SpringerVerlag, Berlin, pp 333-388
- Kunz TH (1982) Roosting ecology of bats. In: Kunz TH (ed) *Ecology of bats*. Plenum Press, New York, pp 1-51
- Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) *Bat ecology*. Univ Chicago Press, Chicago, pp 3-89
- Leroy EM, Kumulungui B, Pourrut X, Rouquet P, Hassanin A, Yaba P, Délicat A, Paweska JT, Gonzalez J-P, Swanepoel R (2005) Fruit bats as reservoirs of Ebola virus. *Nature* 438:575-576
- Lewis SE (1995) Roost fidelity of bats: A review. *J Mammal* 76:481-496
- Lim BK, Engstrom MD (2004) Mammals of Iwokrama Forest. *Proc Acad Nat Sci Philadelphia* 154:71-108
- Linhares AX, Komeno CA (2000) *Trichobius joblingi*, *Aspidoptera falcata*, and *Megistopoda proxima* (Diptera: Streblidae) parasitic on *Carollia perspicillata* and *Sturnira lillium* [sic] (Chiroptera: Phyllostomidae) in Southeastern Brazil: Sex ratios, seasonality, host site preference, and effect of parasitism on the host. *J Parasitol* 86:167-170
- Maa TC (1965) Ascodipterinae of Africa (Diptera: Streblidae). *J Med Entomol* 4:311-326
- Maa TC, Peterson BV (1987) Hippoboscidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) *Manual of Nearctic Diptera*, vol 2. Research Branch, Agriculture Canada, pp 1271-1281
- Marshall AG (1970) The life cycle of *Basilisa hispida* Theodor 1957 (Diptera: Nycteribiidae) in Malaysia. *Parasitology* 61:1-18
- Marshall AG (1971) The ecology of *Basilisa hispida* (Diptera: Nycteribiidae) in Malaysia. *J Anim Ecol* 40:141-154
- Marshall AG (1976) Host-specificity amongst arthropods ectoparasitic upon mammals and birds in the New Hebrides. *Ecol Entomol* 1:189-199

- Marshall AG (1980a) The function of combs in ectoparasitic insects. In: Traub R, Starcke H (eds) Fleas. Proceedings of the international conference on fleas. Ashton Wold/Peterborough/UK/21–25 June 1977. Balkema, Rotterdam, pp 79–87
- Marshall AG (1980b) The comparative ecology of insects ectoparasitic upon bats in west Malaysia. In: Wilson DE, Gardner AL (eds) Proceedings. Fifth international bat research conference. Texas Tech Press, Lubbock, pp 135–142
- Marshall AG (1981) The ecology of ectoparasitic insects. Acad Press, New York
- McAlpine JF (1989) Phylogeny and classification of the Muscomorpha. In: McAlpine JF (ed) Manual of North American Diptera, vol 3. Research Branch, Agriculture Canada, pp 1397–1518
- Nirmala X, Hypsa V, Zurovec M (2001) Molecular phylogeny of Calyptratae (Diptera: Brachycera): The evolution of 18S and 16S ribosomal rDNAs in higher dipterans and their use in phylogenetic inference. *Insect Mol Biol* 10:475–485
- Overall WL (1980) Host-relations of the bat fly *Megistopoda aranea* (Diptera: Streblidae) in Panama. *Univ Kans Sci Bull* 52:1–20
- Patterson BD, Ballard JWO, Wenzel RL (1998) Distributional evidence for cospeciation between Neotropical bats and their bat fly ectoparasites. *Stud Neotrop Fauna Env* 33:76–84
- Poulin R (1998) Evolutionary ecology of parasites: From individuals to communities. Chapman and Hall, London
- Reisen WK, Kennedy ML, Reisen NT (1976) Winter ecology of ectoparasites collected from hibernating *Myotis velifer* (Allen) in southwestern Oklahoma (Chiroptera: Vespertilionidae). *J Parasitol* 62:628–635
- Reiczigel J, Rozsa L (1998) Host-mediated site segregation of ectoparasites: an individual-based simulation study. *J Parasitol* 84:491–498
- Roberts LS, Janovy Jr J (2000) Foundations of parasitology, 6<sup>th</sup> ed. McGraw Hill, Chicago
- Ross A (1960) Notes on *Trichobius corynorhini* on hibernating bats (Diptera: Streblidae). *Wasmann J Biol* 18:271–272
- Peterson BV, Wenzel RL (1987) Nycteribiidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of Nearctic Diptera, vol 2. Research Branch, Agriculture Canada, pp 1283–1291
- ter Hofstede HM, Fenton MB, Whitaker Jr JO (2004) Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera). *Can J Zool* 82:616–626
- ter Hofstede HM, Fenton MB (2005) Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. *J Zool Lond* 266:333–340
- Theodor O (1957) Parasitic adaptation and host-parasite specificity in the pupiparous Diptera. In: Mayr E (ed) First symposium on host specificity among parasites of vertebrates. Institut de Zoologie, Université de Neuchâtel, Switzerland, pp 50–63
- Theodor O (1967) An illustrated catalogue of the Rothschild collection of Nycteribiidae. Trust Brit Nat Hist Mus, London

- Theodor O, Moscona A (1954) On bat parasites in Palestine. I. Nycteribiidae, Streblidae, Hemiptera, Siphonaptera. *Parasitology* 44:157–245
- Traub R (1972) The relationship between spines, combs and other skeletal features of fleas (Siphonaptera) and the vestiture, affinities and habits of their hosts. *J Med Entomol* 9:601
- Wenzel RL (1976) The streblid batflies of Venezuela (Diptera: Streblidae). *B Young Univ Sci Bull* 20:1–177
- Wenzel RL, Tipton VJ (1966) Some relationships between mammal hosts and their ectoparasites. In: Wenzel RL, Tipton VJ (eds) *Ectoparasites of Panama*. *Field Mus Nat Hist, Chicago*, pp 677–723
- Wenzel RL, Tipton VJ, Kiewlicz A (1966) The streblid batflies of Panama (Diptera: Calypterae: Streblidae). In: Wenzel, RL, Tipton VJ (eds) *Ectoparasites of Panama*. *Field Mus Nat Hist, Chicago*, pp 405–675
- Whitaker Jr JO, Ritzi CM, Dick CW (in press) Collecting and preserving ectoparasites for ecological study. In: Kunz TH (eds) *Ecological and behavioral methods for the study of bats*, 2<sup>nd</sup> edn. *Smithsonian Inst Press, Washington*
- Yeates DK, Wiegmann BM (1999) Congruence and controversy: Toward a higher-level phylogeny of Diptera. *Ann Rev Entomol* 44:397–428

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# Micromammals and Macroparasites

From Evolutionary Ecology to Management

With 79 Figures

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*Cover illustrations:* Micromammals: a lagomorph, *Ochotona daurica* (middle left); a rodent, *Gerbillus dasyurus* (middle right); an insectivore, *Suncus murinus* (bottom right; photographs taken by Georgy I. Shenbrot, Ben Gurion University of the Negev, Israel). Macroparasites: a cestode, *Meggittina cricetomydis* (top); a nematode, *Heligmosomoides glareoli* (bottom left; photographs taken by Boyko Georgiev, Natural History Museum, UK, and Central Laboratory of General Ecology, Bulgarian Academy of Sciences, Bulgaria); capitulum of a nymph of a tick, *Haemaphysalis leporispalustris* (middle center; scanning electron micrograph taken by Lance A. Durden, Georgia Southern University, USA).

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